

PART 2

LM3-EUTRO

Appendix 2.3.1. Development of LM3-Eutro Equations

Important characteristics of eutrophication modeling are the many interactions among nutrients, plankton, and sediments and the transformation reactions describing the conversions between dissolved and particulate phases. In a modeling framework, each interaction is described as a mathematical equation, and the challenge is to define a relatively simple expression to approximate more complex biochemical processes. The model equations used in LM3-Eutro are described here.

A2.3.1 Phytoplankton Growth

Although several phytoplankton groups are present in Lake Michigan, the lake is dominated by diatoms and flagellates. The major differences between these classes are silica dependence by the diatoms, settling rates, carbon content, and growth rates at different times of the year. It has been speculated that diatoms grow faster than “non-diatoms” and that they grow better at cold temperatures because their blooms are usually observed during the spring in the Great Lakes. The kinetic equations used in this model are based on the WASP family of models (Thomann and Di Toro, 1975; Di Toro and Connolly, 1980; Rodgers and Salisbury, 1981a, b) and CEQUAL-ICM, developed by the U.S. Army Corps of Engineers (Cerco and Cole, 1993). These equations do not include settling rates. Settling was included as part of the model transport in the LM3 model framework. The basic phytoplankton growth equation can be written as:

Net Production = Gross Production - Mortality

$$\frac{dP}{dt} = (k_g - k_d) P - k_{gz} Z \quad (\text{A2.3.1.1})$$

where

P = phytoplankton concentration (mass/volume)

t = time

k_g = phytoplankton growth rate (1/time)

k_d = phytoplankton mortality rate (1/time)

k_{gz} = predation rate (1/time)

Z = zooplankton concentration (mass/volume)

The growth rate can be written as:

$$k_g = k_{gmax} f(N) f(T) f(I) \quad (\text{A2.3.1.2})$$

where

k_{gmax} = optimum growth rate (1/time)

$f(N)$ = nutrient growth dependency

$f(I)$ = light growth dependency

$f(T)$ = temperature growth dependency

For the nutrient growth dependency, we used the standard Monod equation, but treated diatoms slightly differently than non-diatoms. Assuming that

a fraction of the dissolved organic phosphorus (DOP) was readily available for algal uptake, available phosphorus, P_{av} , was defined as follows:

$$P_{av} = SRP + f_{DOP} DOP \quad (A2.3.1.3)$$

where

f_{DOP} = fraction of available DOP

DOP = dissolved organic phosphorus concentration (mass/volume)

For the non-diatoms, the Liebig's law of minimum applied with no silica dependency.

$$f(N) = \min \left[\left(\frac{NH_4 + NO_3}{k_{sat-N} + NH_4 + NO_3} \right), \left(\frac{P_{av}}{k_{sat-P} + P_{av}} \right) \right] \quad (A2.3.1.4)$$

where

NH_3 = ammonia concentration (mass/volume)

NO_3 = nitrate concentration (mass/volume)

k_{sat-N} = half-saturation coefficient for nitrogen uptake (mass/volume)

k_{sat-P} = half-saturation coefficient for phosphorus uptake (mass/volume)

The diatoms were described using the product of the silica limitation and the minimum of nitrogen and phosphorus:

$$f(N) = \left(\frac{Si}{k_{sat-Si} + Si} \right) \min \left[\left(\frac{NH_4 + NO_3}{k_{sat-N} + NH_4 + NO_3} \right), \left(\frac{P_{av}}{k_{sat-P} + P_{av}} \right) \right] \quad (A2.3.1.5)$$

where

k_{sat-Si} = half-saturation coefficient for silica uptake

The temperature dependency was expressed using an equation analogous to the Arrhenius temperature correction. Thus:

$$f(T) = \begin{cases} \exp^{-k_{tg1} (T - T_M)^2} & \text{where } T \leq T_M \\ \exp^{-k_{tg2} (T_M - T)^2} & \text{where } T > T_M \end{cases} \quad (A2.3.1.6)$$

where

k_{tg1} = temperature effect below optimum temperature ($^{\circ}C$)

k_{tg2} = temperature effect above optimum temperature ($^{\circ}C$)

T_M = optimum temperature for phytoplankton growth ($^{\circ}C$)

T = temperature ($^{\circ}C$)

A number of equations had been proposed to describe the effect of light intensity on phytoplankton production. Steele's equation (Steele, 1962) is one of the most commonly used expressions, while a light saturation equation (similar to the Monod equation) is also frequently used (Di Toro *et al.*, 1971). In this model, light dependency is described according to Steele's equation.

$$f(I) = \frac{I}{I_s} \exp \left[\frac{-I}{I_s} + 1 \right] \quad (A2.3.1.7)$$

where

$f(I)$ = light limitation (fraction between 0 and 1)

I = incident solar light intensity (energy/time/area)

I_s = saturating light intensity (energy/time/area)

The Beer-Lambert equation was used to estimate the light penetration in the water:

$$I_z = I_0 \exp(-k_e z) \quad (A2.3.1.8)$$

where

I_z = the light intensity at depth z (energy/time/area)

I_0 = the surface light intensity (energy/time/area)

k_e = light extinction coefficient (1/length)

z = depth (length)

Substituting Equation (A2.3.1.8) into Equation (A2.3.1.7):

$$f(I(z)) = \frac{I_0 \exp(-k_e z)}{I_s} \exp\left[\frac{I_0 \exp(-k_e z)}{I_s} + 1\right] \quad (\text{A2.3.1.9})$$

This equation calculated the light limitation at an instantaneous time and at a specific depth. However, the need to estimate the light limitation at a certain cell (with a given depth range) and over a time period (the time step) was desired. Thus, it was necessary to integrate this equation over time and depth. Di Toro *et al.* (1971) formulated an equation assuming a constant light intensity over photoperiod. They integrated Steele's equation (Equation A2.3.1.9) over a 24-hour period and the total depth of a segment.

$$f(I_a) = \frac{2.718 fd}{k_e \Delta z} [\exp(-\alpha_1) - \exp(-\alpha_0)] \quad (\text{A2.3.1.10})$$

where

$$\alpha_0 = \frac{I_a}{I_s} \exp(-k_e z_1) \quad (\text{A2.3.1.11})$$

$$\alpha_1 = \frac{I_a}{I_s} \exp(-k_e z_2) \quad (\text{A2.3.1.12})$$

and

fd = the photoperiod (time)

I_a = average light intensity over the photoperiod (energy/time/area)

This approach is still very commonly used, although it has been criticized for losing the power to represent midday surface inhibition (Di Toro *et al.*, 1971;

Kremer and Nixon, 1978). In our model, we had the luxury of performing variable time averaging from hourly to 12-hour averages and observing the difference.

However, if one wanted to estimate the light limitation for less than a day and the average light intensity of that period was known, one can solve Steele's equation as follows (note: it is only integrated over depth, but not over time):

$$f(I_a) = \int_{z_1}^{z_2} \frac{1}{z} \left(\frac{I_a \exp(-k_e z)}{I_s} \exp\left[\frac{-I_a \exp(-k_e z)}{I_s} + 1\right] \right) dz \quad (\text{A2.3.1.13})$$

The solution was almost the same as Equation (A2.3.1.10), without the fraction of daylight in the equation.

$$f(I_a) = \frac{2.718}{k_e \Delta z} [\exp(-\alpha_1) - \exp(-\alpha_0)] \quad (\text{A2.3.1.14})$$

The average light intensity (I_a) here can be calculated as follows:

$$I_a = \frac{\int I_0(t) dt}{\int dt} \quad (\text{A2.3.1.15})$$

where

I_0 = measured incident solar radiation (energy/time/area)

t = time

and can, thus, be approximated by:

$$I_a = \frac{1}{n} \sum_{i=1}^n I_0(t_n) \quad (\text{A2.3.1.16})$$

where

n = number of discrete time intervals at which I_0 is measured.

A2.3.2 Zooplankton Kinetics

Zooplankton predation is important in regulating the phytoplankton densities in Lake Michigan, especially during the stratified summer months (Scavia *et al.*, 1988). Lake Michigan zooplankton are dominated by herbivorous species, with copepods making up the majority of the total biomass for most of the year. However, cladocerans exhibit significant peaks in the late summer and fall. Due to the limited zooplankton data reported for the lake and the lack of kinetic laboratory and field studies for Lake Michigan zooplankton populations, we avoided complex zooplankton equations (e.g., Bowie *et al.*, 1985), and chose a relatively simple formulation. The equations describing herbivorous zooplankton growth were based on formulations from the literature (Bowie *et al.*, 1985; Di Toro and Connolly, 1980; Di Toro and Matystik, 1980; Thomann and Mueller, 1987). Carnivorous zooplankton were not directly simulated here, but were represented in a herbivorous zooplankton mortality term.

The following equation was used:

$$\frac{dZ}{dt} = (\varepsilon k_{gz} - k_{dz}) Z \quad (\text{A2.3.1.17})$$

where

Z = zooplankton concentration (mass/volume)

t = time

k_{gz} = growth rate (1/time)

k_{dz} = mortality (1/time)

ε = growth efficiency

$$k_{gz} = k_{gzmax} \left(\frac{P}{k_s + P} \right) \theta^{T - T_{rz}} \quad (\text{A2.3.1.18})$$

where

k_{gzmax} = maximum growth rate (1/time)

P = diatom and greens concentration (mass/volume)

k_s = half-saturation coefficient (mass/volume)

θ = temperature correction factor

T_{rz} = reference temperature (°C)

The maximum growth rate is a term that lumps the filtration and assimilation rates into a single term. The mortality term lumps respiration, excretion, and higher predation in a single term. We can, thus, write the overall equation:

$$\frac{dZ}{dt} = \left[\varepsilon k_{gzmax} \frac{P}{k_s + P} \theta^{T - T_{rz}} - k_{dz} \right] Z \quad (\text{A2.3.1.19})$$

A2.3.3 Carbon Interactions

Several carbon interactions were described in the model, including phytoplankton and zooplankton carbon, carbon loads from tributaries, shoreline erosion, and detrital carbon from plankton. The carbon state variables in this model were diatom, non-diatom, and zooplankton carbon; labile detrital carbon; refractory detrital carbon; and dissolved organic carbon (DOC). Carbon dioxide (CO₂) was not simulated, although a mineralization reaction was included. Diatom and non-diatom carbon were simulated, as described in the previous section. Labile detrital carbon referred to the organic detrital carbon from the phytoplankton species which breaks down, as the name implies, relatively rapidly. In contrast, the refractory detrital carbon is the combination of the fraction of the plankton breaking down, as well as other forms of organic carbon in the system, e.g., carbon from tributaries, the sediments, etc. These forms of carbon break down slowly, but are not totally refractory. In the equation, we specify the fractions of labile and refractory carbon. We assumed that phytoplankton utilizes CO₂ as the carbon source during photosynthesis and releases carbon as dissolved (CO₂ and DOC) and particulate (refractory organic carbon [ROC] and labile organic carbon [LOC]) forms.

Phytoplankton Mortality and Decay

Phytoplankton respiration and non-predatory mortality were grouped together in the model as a "mortality" term. The release of carbon as CO₂ from these processes was split into different fractions of DOC and POC.

$$\frac{dDOC}{dt} = f_{cdm} k_d P \quad (A2.3.1.20)$$

where

f_{cdm} = fraction of DOC from mortality

$$\frac{dROC}{dt} = f_{crm} k_d P \quad (A2.3.1.21)$$

where

f_{crm} = fraction of ROC from mortality

$$\frac{dLOC}{dt} = f_{clm} k_d P \quad (A2.3.1.22)$$

where

f_{clm} = fraction of LOC from mortality

However, phytoplankton carbon was also converted to detrital and DOC through predation (messy feeding) and zooplankton-imposed mortality.

$$\frac{dDOC}{dt} = f_{cdp} (1 - \varepsilon) k_{gz} Z \quad (A2.3.1.23)$$

where

f_{cdp} = fraction of DOC from predation

$$\frac{dROC}{dt} = f_{crp} (1 - \varepsilon) k_{gz} Z \quad (A2.3.1.24)$$

where

f_{crp} = fraction of ROC from predation

$$\frac{dLOC}{dt} = f_{clp} (1 - \varepsilon) k_{gz} Z \quad (A2.3.1.25)$$

where

f_{clp} = fraction of LOC from predation

Zooplankton Mortality and Decay

The zooplankton mortality term included respiration, non-predatory mortality, and predation (we did not

simulate any higher predation such as carnivorous zooplankton). We assumed that the detrital zooplankton carbon consisted of dissolved, labile, particulate, and refractory particulate fractions.

$$\frac{dDOC}{dt} = f_{cdz} k_{dz} Z \quad (A2.3.1.26)$$

where

f_{cdz} = fraction of DOC from zooplankton mortality

$$\frac{dLOC}{dt} = f_{clz} k_{dz} Z \quad (A2.3.1.27)$$

where

f_{clz} = fraction of LOC from zooplankton mortality

$$\frac{dROC}{dt} = f_{crz} k_{dz} Z \quad (A2.3.1.28)$$

where

f_{crz} = fraction of ROC from zooplankton mortality

Particulate fractions (both labile and refractory) were hydrolyzed to DOC, while DOC mineralized to CO₂.

Since we did not explicitly model bacteria in this model, their breakdown of carbon was modeled by including a dependency on the phytoplankton, which acted as a surrogate of the heterotrophic bacterial activity in the lake. We also calculated a temperature limitation to the hydrolysis and mineralization. The equations can be written as follows:

$$Tf_{mnl} = \exp [Tk_{mnl} (T - Tr_{mnl})] \quad (A2.3.1.29)$$

$$Tf_{hdr} = \exp [Tk_{hdr} (T - Tr_{hdr})] \quad (A2.3.1.30)$$

where

Tf_{mnl} = temperature correction for mineralization (°C)

Tf_{hdr} = temperature correction for hydrolysis (°C)

Tk_{mnl} = mineralization temperature coefficient (°C⁻¹)

Tk_{hdr} = hydrolysis temperature coefficient (°C⁻¹)

Tr_{mnl} = optimum temperature correction for mineralization (°C)

Tr_{hdr} = optimum temperature correction for hydrolysis (°C)

$$- \frac{dDOC}{dt} = Tf_{mnl} (k_{dc} + k_{dcp}) P DOC \quad (A2.3.1.31)$$

$$- \frac{dROC}{dt} = Tf_{hdr} (k_{rc} + k_{rcp}) P ROC \quad (A2.3.1.32)$$

$$- \frac{dLOC}{dt} = Tf_{hdr} (k_{lc} + k_{lcp}) P LOC \quad (A2.3.1.33)$$

where

k_{dc} = DOC minimum mineralization rate (1/time)

k_{dcp} = DOC mineralization relating to phytoplankton (volume/mass/time)

k_{rc} = ROC minimum hydrolysis rate (1/time)

k_{rcp} = ROC hydrolysis relating to phytoplankton (volume/mass/time)

k_{lc} = LOC minimum hydrolysis rate (time⁻¹)

k_{lcp} = LOC hydrolysis relating to phytoplankton (volume/mass/time)

Examining the last two equations, we calculated that the gain in DOC equaled the sum of the loss of ROC and LOC.

A2.3.4 Phosphorus

In our model, phosphorus existed as one of four species (in addition to being tied up in the phytoplankton). Note that all four forms were in the same oxidation state, thus, no oxidation reactions occurred. The forms were soluble reactive phosphorus (SRP), DOP, and two forms of particulate organic phosphorus (POP) – a labile (LOP) and a refractory (ROP) form. SRP and a small fraction of the DOP were taken up by the phytoplankton during production (photosynthesis). It was released due to mortality and predation.

Particulate phosphorus was hydrolyzed to DOP and DOP to SRP.

Phosphorus Uptake by Phytoplankton

Soluble Reactive Phosphorus Uptake:

$$\frac{dSRP}{dt} = - r_{pc} k_g P \frac{SRP}{SRP + f_{DOP} DOP} \quad (A2.3.1.34)$$

where

r_{pc} = the P:C ratio

Dissolve Organic Phosphorus Uptake:

$$\frac{dDOP}{dt} = - r_{pc} k_g P \frac{f_{DOP} DOP}{f_{DOP} DOP + SRP} \quad (A2.3.1.35)$$

where

r_{pc} = the P:C ratio

An interesting concept, common in many phytoplankton models, is the way in which the nutrients, including phosphorus, are accounted for within the phytoplankton. The model kept track of the carbon and used a constant carbon:nutrient relationship to make these determinations.

Phytoplankton in the water column were hydrolyzed and mineralized to all four phosphorus forms. During algal metabolic/mortality processes, phytoplankton-phosphorus was converted to particulate and dissolved organic forms as well as directly to SRP.

$$\frac{dSRP}{dt} = r_{pc} f_{srp} k_d P \quad (A2.3.1.36)$$

$$\frac{dDOP}{dt} = r_{pc} f_{dop} k_d P \quad (A2.3.1.37)$$

$$\frac{dLOP}{dt} = r_{pc} f_{lop} k_d P \quad (A2.3.1.38)$$

$$\frac{dROP}{dt} = r_{pc} f_{rop} k_d P \quad (A2.3.1.39)$$

where

f_{srp} = fraction SRP from metabolic processes

f_{dop} = fraction DOP from metabolic processes

f_{lop} = fraction of LOP from metabolic processes

f_{rop} = fraction of ROP from metabolic processes

During the phytoplankton predation, zooplankton assimilated only a fraction of the phytoplankton and the remainder of the detrital phytoplankton was released directly to the water. This process is commonly referred to as “messy feeding.” The phosphorus was released in both the dissolved and particulate forms.

$$\frac{dSRP}{dt} = f_{plp} (1 - \varepsilon) r_{pc} k_{gz} Z \quad (A2.3.1.40)$$

$$\frac{dDOP}{dt} = f_{pdp} (1 - \varepsilon) r_{pc} k_{gz} Z \quad (A2.3.1.41)$$

$$\frac{dROP}{dt} = f_{prp} (1 - \varepsilon) r_{pc} k_{gz} Z \quad (A2.3.1.42)$$

$$\frac{dLOP}{dt} = f_{plp} (1 - \varepsilon) r_{pc} k_{gz} Z \quad (A2.3.1.43)$$

where

f_{pip} = fraction of SRP from predation

f_{pdp} = fraction of DOP from predation

f_{plp} = fraction of LOP from predation

f_{prp} = fraction of ROP from predation

The model also included equations to describe zooplankton mortality. Phosphorus was released to the water column in both the dissolved and particulate forms.

$$\frac{dSRP}{dt} = f_{plz} r_{pc} k_{dz} Z \quad (A2.3.1.44)$$

$$\frac{dDOP}{dt} = f_{pdz} r_{pc} k_{dz} Z \quad (A2.3.1.45)$$

$$\frac{dLOP}{dt} = f_{plz} r_{pc} k_{dz} Z \quad (A2.3.1.46)$$

$$\frac{dROP}{dt} = f_{prz} r_{pc} k_{dz} Z \quad (A2.3.1.47)$$

where

f_{piz} = fraction of SRP from zooplankton mortality

f_{pdz} = fraction of DOP from zooplankton mortality

f_{plz} = fraction of LOP from zooplankton mortality

f_{prz} = fraction of ROP from zooplankton mortality

Particulate phosphorus was hydrolyzed to DOP and DOP was mineralized back to SRP as follows:

$$- \frac{dDOP}{dt} = k_{dp} + \left(k_{dpa} P \frac{k_{sat-pt}}{SRP + k_{sat-pt}} \right) \quad (A2.3.1.48)$$

$$- \frac{dLOP}{dt} = k_{lp} + \left(k_{lpa} P \frac{k_{sat-pt}}{SRP + k_{sat-pt}} \right) \quad (A2.3.1.49)$$

$$- \frac{dROP}{dt} = k_{rp} + \left(k_{rpa} P \frac{k_{sat-pt}}{SRP + k_{sat-pt}} \right) \quad (A2.3.1.50)$$

where

k_{dp} = DOP mineralization coefficient (1/time)

k_{lp} = LOP hydrolysis coefficient (1/time)

k_{rp} = ROP hydrolysis coefficient (1/time)

k_{dpa} = DOP mineralization coefficient algal dependence (volume/mass/time)

k_{lpa} = LOP hydrolysis coefficient algal dependence (volume/mass/time)

k_{rpa} = ROP hydrolysis coefficient algal dependence (volume/mass/time)

k_{sat-pt} = mean saturation coefficient of algal classes for SRP

A2.3.5 Nitrogen

The transformation of nitrogen was similar to phosphorus, although nitrogen existed in more than one oxidation state. Algal nitrogen was released as two forms of particulate organic nitrogen (labile [LON], refractory [RON]), dissolved organic nitrogen (DON), and ammonia (NH_4). Particulate forms were hydrolyzed to DON. DON was further mineralized to NH_4 and NH_4 is oxidized to nitrate (NO_3).

In our model, we assumed that phytoplankton had no preference between NH_4 and NO_3 as a nitrogen source.

$$\frac{dDIN}{dt} = -r_{nc} k_g P \quad (\text{A2.3.1.51})$$

where

$$DIN = \text{NH}_4 + \text{NO}_3$$

$$r_{nc} = \text{N:C ration}$$

Because we assumed no preference, then

$$\frac{d\text{NH}_4}{dt} = -\left[\frac{\text{NH}_4}{DIN}\right] r_{nc} k_g P \quad (\text{A2.3.1.52})$$

$$\frac{d\text{NO}_3}{dt} = -\left[\frac{\text{NO}_3}{DIN}\right] r_{nc} k_g P \quad (\text{A2.3.1.53})$$

Similar to phosphorus, nitrogen bound to phytoplankton can be released as particulate organic, dissolved organic and NH_4 forms.

$$\frac{d\text{NH}_4}{dt} = r_{nc} f_{din} k_d P \quad (\text{A2.3.1.54})$$

$$\frac{dDON}{dt} = r_{nc} f_{don} k_d P \quad (\text{A2.3.1.55})$$

$$\frac{dLON}{dt} = r_{nc} f_{lon} k_d P \quad (\text{A2.3.1.56})$$

$$\frac{dRON}{dt} = r_{nc} f_{ron} k_d P \quad (\text{A2.3.1.57})$$

where

$$f_{din} = \text{fraction } \text{NH}_4 \text{ from metabolic processes}$$

$$f_{don} = \text{fraction DON from metabolic processes}$$

$$f_{lon} = \text{fraction LON from metabolic processes}$$

$$f_{ron} = \text{fraction RON from metabolic processes}$$

As described for carbon and phosphorus, the nitrogen balance was affected by the zooplankton through “messy feeding” and zooplankton mortality.

$$\frac{d\text{NH}_4}{dt} = f_{nlp} (1 - \epsilon) r_{nc} k_{gz} Z \quad (\text{A2.3.1.58})$$

$$\frac{dDON}{dt} = f_{ndp} (1 - \epsilon) r_{nc} k_{gz} Z \quad (\text{A2.3.1.59})$$

$$\frac{dLON}{dt} = f_{nlp} (1 - \epsilon) r_{nc} k_{gz} Z \quad (\text{A2.3.1.60})$$

$$\frac{dRON}{dt} = f_{nrp} (1 - \epsilon) r_{nc} k_{gz} Z \quad (\text{A2.3.1.61})$$

where

$$f_{nlp} = \text{fraction of } \text{NH}_4 \text{ from predation}$$

$$f_{ndp} = \text{fraction of DON from predation}$$

$$f_{nlp} = \text{fraction of LON from predation}$$

$$f_{nrp} = \text{fraction of RON from predation}$$

The release of nitrogen during zooplankton mortality can be expressed similarly to the phosphorus.

$$\frac{d\text{NH}_4}{dt} = f_{niz} r_{nc} k_{dz} Z \quad (\text{A2.3.1.62})$$

$$\frac{dDON}{dt} = f_{ndz} r_{nc} k_{dz} Z \quad (\text{A2.3.1.63})$$

$$\frac{dLON}{dt} = f_{niz} r_{nc} k_{dz} Z \quad (\text{A2.3.1.64})$$

$$\frac{dRON}{dt} = f_{nrz} r_{nc} k_{dz} Z \quad (A2.3.1.65)$$

where

f_{niz} = fraction of NH_4 from zooplankton mortality

f_{ndz} = fraction of DON from zooplankton mortality

f_{nlz} = fraction of LON from zooplankton mortality

f_{nrz} = fraction of RON from zooplankton mortality

A2.3.6 Silica

The behavior of silica was similar to that of phosphorus and nitrogen. Two silica species, biogenic silica (SU) and available silica (SA), were simulated in the lake. Dissolved silica was utilized by phytoplankton, while both dissolved and biogenic silica were released *via* phytoplankton mortality, predation upon phytoplankton by zooplankton, and zooplankton mortality. The major difference from the other nutrients was that only diatoms had a silica dependency.

The diatom silica consumption can be written as follows:

$$\frac{dSA}{dt} = - r_{sc} k_g P \quad (A2.3.1.66)$$

where

r_{sc} = Si:C ratio

Note that in all the silica equations, the variable phosphorus refers only to the diatom concentration. Like the other nutrients, silica was released *via* diatom mortality.

$$\frac{dSU}{dt} = - r_{sc} k_d P \quad (A2.3.1.67)$$

Both classes of silica could be released *via* zooplankton predation.

$$\frac{dSA}{dt} = - f_{sap} r_{sc} k_{gz} \quad (A2.3.1.68)$$

$$\frac{dSU}{dt} = - f_{sup} r_{sc} k_{gz} \quad (A2.3.1.69)$$

where

f_{sap} = fraction of SA from predation

f_{sup} = fraction of SU from predation

We assumed that no silica accumulated within the zooplankton so there were no terms for silica release from zooplankton mortality.

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